Reproductive Behavior in the Squid *Sepioteuthis australis* From South Australia: Ethogram of Reproductive Body Patterns

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Abstract. Squids use a diverse range of body patterns for communication. Each pattern consists of a series of chromatic, postural, and locomotor components that are under neural control and can change within fractions of a second. Here we describe an ethogram of 48 body pattern components from *in situ* observations of reproductively active *Sepioteuthis australis*. In addition, we identify the total time and average duration that each component is shown, to a resolution of 1 s. Our results suggest that only a few components (*e.g.*, "Golden epaulettes," "Stitchwork fins," and "Rigid arms") are temporally common, that is, shown for more than 80% of the time. In contrast to the component classification reported for other species of squid, for this species we suggest a classification system consisting of "short acute" (lasting for < 10 s); some of these same components were also classified as "medium acute" (11–60 s) or "chronic" (> 60 s). Several body patterning components were previously unreported, as were some of the combinations observed. The significance of these patterning components is discussed within the context of the associated behaviors of the squid on the spawning grounds.

Introduction

Cephalopod behavior involves elaborate displays characterized by many visually apparent body patterns (Moynihan and Rodaniche, 1982; Hanlon, 1988; Hanlon *et al.*, 1994, 1999; Hanlon and Messenger, 1996). In squid, each body pattern is a combination of postural, locomotor, or chromatic components that together constitute the total appearance of the animal (Packard and Sanders, 1969, 1971; Packard and Hochberg, 1977; Hanlon, 1982; Roper and Hochberg, 1988; Hanlon *et al.*, 1994, 1999; Hanlon and Messenger, 1996). Of the three types, the most conspicuous and diverse to the human observer are the chromatic components. Chromatic changes result from neuromuscular expansion or retraction of pigmented chromatophore organs in the dermis of the skin (Boycott, 1953; Hanlon, 1982; Packard, 1982, Messenger, 2001). Dark chromatic components arise from the expansion of chromatophores, whereas light chromatic components are the result of retraction of chromatophores to reveal the translucent skin or iridescent reflecting cells (Hanlon, 1982; Hanlon and Messenger, 1996; Messenger, 2001). Postural components denote the postures of arms, tentacles, head, eyes, mantle, and fins; and locomotor components describe movement of the whole animal (Hanlon and Messenger, 1996). Squid display multiple combinations of each component type that may last for several seconds ("acute patterns" *sensu* Packard and Hochberg, 1977; Hanlon and Messenger, 1996), or minutes to hours ("chronic patterns" *sensu* Hanlon and Messenger, 1996). Unfortunately, the classification of squid body patterns is not a simple task. Each chromatic component may be displayed alone, or combined with other components (simultaneously or in sequence) to generate the overall skin pattern of an individual (Hanlon *et al.*, 1994, 1999; Mather and Mather, 1994). Thus, to analyze the nature of squid behavior, body components must first be cataloged, then each combination of components analyzed with respect to the circumstances in which each occurs (Mather and Mather 1994).

Body patterning and reproductive behavior are important tools in quantitative behavioral analysis, in the development of taxonomic identification keys, and for phylogenetic analyses of chromatic expression (Hanlon, 1988). Cephalopod

body patterns have been studied for many decades, and the suite of body pattern components (ethogram) found in squids has been described for species such as *Sepioteuthis sepioidea* (Moynihan and Rodaniche, 1982), *Loligo vulgaris reynaudii* (Hanlon *et al.*, 1994), *Loligo pealeii* (Hanlon *et al.*, 1999), and several others (table 3.2 in Hanlon and Messenger, 1996).

The commercially important squid *Sepioteuthis australis* spawns throughout the year (Pecl, 2000, 2001), with numbers of spawning adults in shallow coastal areas known to increase during warmer months. Current behavioral research on this species is limited to two preliminary observations of spawning activity, neither of which describes the repertoire of body patterns (Larcombe and Russell, 1971; Jantzen and Havenhand, 2003). In this study, we document and identify 48 components characteristic of *S. australis* reproductive behavior and describe the behaviors associated with each component. In addition, we analyze the occurrence, duration, and frequency of each component.

Materials and Methods

Mating behavior of *Sepioteuthis australis* in the field was observed by scuba and directly from the surface. The presence of divers close to focal animals (< 30 cm) caused no apparent alteration in squid behavior (compared with individuals observed from afar). Observations were therefore routinely made at a distance of less than 2 m.

Reproductively active individuals of *S. australis* were observed by scuba diving and snorkeling during daylight hours on spawning grounds between Marino and Hallet Cove, South Australia (138°29' E, 38°02' S; see Jantzen and Havenhand, 2003, for a description of the site) over three consecutive spawning seasons (September to March) between September 1999 and February 2002. Digital video data were obtained from 50 dives over an 18-week period from November 2000 to March 2001.

Ethogram of reproductive body patterns

Reproductive behavior was recorded with a Sony TV120 digital video camera (Sony Corporation, New York) in an Amphibico (Amphibico, Quebec, Canada) housing. Sampling protocols followed those described by Martin and Bateson (1993), which included small amounts of *ad libitum* sampling of specific behaviors. However, the primary sampling method was focal-animal sampling, which involved recording all interactions and behaviors of haphazardly chosen paired individuals for up to 1.5 h. Because males and females are close together when paired, analysis of the focal sampling of one individual provided information on the corresponding behavior of its mate.

Images of behavior were analyzed frame by frame (25 frames $\cdot$ s^{-1}) on a high-resolution large-screen color monitor. Each video was analyzed three times to identify postural, locomotor, or chromatic components. All components were assigned a name based either on established component nomenclature for other cephalopod species (Corner and Moore, 1980; Hanlon, 1982, 1988; Moynihan and Rodaniche, 1982; Moynihan, 1985; Yang *et al.*, 1986; Porteiro *et al.*, 1990; Hanlon *et al.*, 1994, 1999; Jantzen and Havenhand, 2003); or, where a new chromatic component was identified, on guidelines proposed by Hanlon and Messenger (1996) in which transverse components are called "bands" or "bars," and lines running longitudinal to the body axis called "stripes" or "streaks." In accordance with convention, only the first letter of each component name was capitalized (Hanlon and Wolterding, 1989).

Still images of selected chromatic and postural components were obtained from digital video using iMovie2 software (Apple Computer, Cupertino, CA). Each chromatic component was then illustrated using CorelDraw 3.0 (Corel Corporation, Ontario, Canada) from a lateral perspective (observations were mostly lateral to the focal animal).

Total component duration

Each chromatic, postural, and locomotor component was scored individually (present, absent, data missing) for each squid at a 1-s-interval scale for the duration of the video, so that the proportion of time each component was displayed could be assessed. Missing values were classed as any points when the body of the squid (or part thereof) was not in the field of view (with the exception of "Oviposition," during which females were obscured by seagrass). All missing data (zeros) were eliminated from the analysis. Because video analysis frequently took several hours, the first two squid pairs analyzed were re-analyzed at the end of the analysis session and compared with the original analysis to ensure consistency in interpretation and data recording. Because significant experimental error in the perception of components may occur between observers in behavioral investigations (Drummond, 1981), all analyses were conducted by the same person (TMJ).

The behavior of 22 focal animals (11 female, 11 male) was recorded for a continuous duration of up to 61 min per pair. The total occurrence of each component (in seconds) was determined with respect to the total number of valid data points (missing values excluded) for each animal. Mean total duration of each component as a proportion of total time observed was calculated from data for individuals that showed the component being analyzed (data for animals not showing a component were omitted). Means generated from fewer than three replicate animals were not included in further analysis. Means and 95% confidence intervals were generated for each component.

Pairwise Student's *t* tests were conducted on the duration of each component shown by males and females within replicate pairs. This procedure tested the hypothesis that

there was no significant difference in mean component duration between sexes. Because this involved multiple unplanned tests with consequent information of Type I errors, a sequential Bonferroni test was conducted on the results from the *t* test to determine significance against the table-wide α-level (Rice, 1989).

Average component duration

The average duration of each component was calculated from the "uninterrupted" data (*i.e.*, excluding all component observations that began or ended due to the beginning or end of video recording, or were interrupted by missing values). Average component duration was calculated for each replicate individual, and a mean value was generated for all females or males. Not all components were shown by each individual; therefore, means from fewer than three replicates were, as before, discarded from the analysis.

As with the data for total component duration, pairwise *t* tests were conducted on the average duration of each component shown by males *versus* females within pairs.

Results

Several hundred reproductively active individuals of *Sepioteuthis australis* were observed in more than 75 h underwater. About 10 h of focal-sampling video observations of behavior were recorded. The number of reproductively active individuals ranged from 2 (a single spawning pair) to more than 45 per dive. From these data we identified 48 separate body components: 17 chromatic (Table 1, Fig. 1), 16 postural (Table 1, Fig. 2), and 15 locomotor (Table 1). Mating, egg deposition, and agonistic contests were all seen on the spawning grounds in the same manner as described previously by Jantzen and Havenhand (2003).

Ethogram of reproductive body patterns

Components that were previously undescribed or differ from those in the literature (Corner and Moore, 1980; Hanlon, 1982, 1988; Moynihan and Rodaniche, 1982; Moynihan, 1985; Yang *et al.*, 1986; Porteiro *et al.*, 1990; Hanlon *et al.*, 1994, 1997, 1999; Jantzen and Havenhand, 2003) are described below. Where components do not differ from existing definitions, the relevant literature has been cited. Unless stated otherwise, components were observed in both sexes, lateral to the focal animal.

Results for individual components are described below, summarized in Table 1, and illustrated in Figures 1 and 2. Combinations of components for typical behaviors are presented in Figure 3. Photographs of common combinations of chromatic and postural components are shown in Figure 4.

1. Light chromatic components

Clear (Hanlon, 1988; Yang *et al.*, 1986; Porteiro *et al.*, 1990; Hanlon *et al.*, 1994, 1999; Cornwell *et al.*, 1997) was rarely observed (three observations from focal sampling; Table 1) and on each occasion was shown alone as a body pattern. **White dorsal stripe** was a lightened stripe in the center of the dorsal mantle and varied in intensity; it either extended along the entire longitudinal length of the dorsal surface or was restricted to the posterior region. This component often began at the posterior region and extended to cover the entire longitudinal dorsal mantle. Without exception, females showed "White dorsal stripe" in combination with "Male-upturned mating" (see below and Fig. 3). **Golden epaulette**s was a lightened band at the most anterior point of the dorsal mantle that occurred as a result of the contraction of chromatophores (referred to as "Dorsal mantle collar iridophores" by Hanlon, 1988; Hanlon *et al.*, 1994, 1999). This was the most prevalent chromatic component (Table 1) and was shown seemingly indiscriminately with almost all other components. **Iridescent sclera** occurred when the iris of the eye became iridescent; it was observed only in agonistic contests between fighting males (Fig. 3), usually in conjunction with "All dark" (see below). **Golden ocular epaulettes** (described above the eye only as "Light eyebrows" or "Glittering brows" in *S. sepioidea*; Moynihan and Rodaniche, 1982; Moynihan 1985) were observed as a lightened region above and/or below the eye. This component was observed only in females (Table 1) and differs from "Iridescent sclera" in that the area adjacent to the eye becomes iridescent.

2. Dark chromatic components

We describe the manner in which dark chromatic components influence overall appearance without reference to the individual contributions of yellow, orange, red, brown, or black chromatophores (Hanlon and Messenger, 1996), which we were not able to analyze.

Plain was shown as a medium brown coloration over the entire body (referred to as "Basic" by Moynihan and Rodaniche, 1982; Moynihan, 1985). This component was more common in females (Table 1) and was especially seen in females that were "Egg passing" (see below). It was also shown by unpaired males attempting to "Male 'sneak' mate" (see below), and by courting pairs. **All Dark** (Hanlon, 1988; Hanlon *et al.*, 1994, 1999; Cornwell *et al.*, 1997) was shown by fighting males that were "Fin beating" (see below and Fig. 3). A variation of the "All dark" component was **Dark mantle,** in which only the mantle was darkened while the head and arms remained "Plain." This component was rare (Table 1), and the behavior associated with it remains unclear.

Although also shown independently, the following four components were all shown together by paired males in the

Table 1

Component duration (minimum and maximum) and frequency of observations of the ethogram of body pattern components for reproductively active males and females of Sepioteuthis australis

| Component | Component duration(s) | | | | Number of observations | | | |
| | Female | | Male | | | | | |
	Min.	Max.	Min.	Max.	Female	Male	Total	Uninterrupted
Chromatic components								
Light:								
1 Clear	1	1	10	10	2	1	3	2
2 White dorsal stripe	1	58	1	29	233	89	322	242
3 Golden epaulettes	1	171	1	338	422	259	681	102
4 Iridescent sclera ($\male$)	-	-	1	11	-	35	35	25
5 Golden ocular epaulettes ($\female$)	2	16	-	-	12	-	12	12
Dark:								
1 Plain	1	58	1	16	150	10	160	106
2 All dark	3	5	1	17	3	30	33	25
3 Dark mantle	2	4	5	5	2	1	3	3
4 Mantle margin stripe	1	31	1	25	12	96	208	143
5 Fin stripe	1	18	1	51	32	113	145	95
6 Dark arm stripes ($\male$)	-	-	1	17	-	73	73	52
7 Stitchwork fins	1	103	1	247	202	232	434	88
8 Dark dorsal stripe	2	10	5	10	4	2	6	6
9 Mottled dorsal mantle	1	30	1	120	91	233	324	135
10 Dark posterior ventral mantle	1	27	1	27	74	19	93	68
11 Shaded eye	1	103	1	156	354	182	536	277
12 Bands	1	151	2	89	153	15	168	75
Postural Components								
1 Drooping arms	1	17	1	81	202	271	473	437
2 Rigid arms	1	507	1	393	731	470	1201	880
3 Upward pointing	1	54	1	42	294	12	306	297
4 Downward pointing	1	12	2	5	142	5	147	143
5 Upward curl	1	17	1	2	23	6	29	29
6 Downward curl	1	6	1	12	60	8	68	68
7 Tentacle curl upward	1	18	3	4	251	3	254	254
8 Tentacle curl downward	1	4	2	4	26	3	29	29
9 Downward splayed arms ($\male$)	-	-	1	10	-	11	11	9
10 Lateral splayed arms ($\male$)	-	-	1	15	-	23	23	21
11 Raised arms	1	32	1	561	138	399	537	416
12 Curled tentacle club ($\female$)	1	29	-	-	84	-	84	76
13 Peristaltic arm flare	1	1	1	1	260	14	274	274
14 Arms in mantle ($\male$)	-	-	4	4	-	1	1	1
15 Forward jetting arms ($\female$)	1	2	-	-	3	-	3	3
16 Egg passing ($\female$)	21	33	-	-	22	-	22	22
Locomotor Components								
1 Forward swimming	1	42	1	38	694	679	1373	1259
2 Backward swimming	1	61	1	76	746	675	1421	1301
3 Hovering	1	152	1	479	778	756	1534	1442
4 Jetting	1	12	1	2	79	7	86	81
5 Turning	1	9	1	16	201	248	449	441
6 Parallel Positioning†	1	175	-	-	417	-	417	399
7 Mate guarding ($\male$)	-	-	1	13	-	108	108	105
8 Parrying ($\male$)	-	-	1	217	-	334	334	260
9 Fin beating ($\male$)	-	-	1	13	-	32	32	30
10 Charging ($\male$)	-	-	1	3	-	7	7	7
11 Oviposition ($\female$)	1	13	-	-	226	-	226	225
12 Male-upturned mating††	-	-	2	4	-	20	20	19
13 Head-to-head mating††	-	-	3	3	-	1	1	1
14 Male-parallel mating††	-	-	4	4	-	1	1	1
15 Male "sneak" mating	-	-	1	2	-	7	7	7

($\female$) = components observed only in females, ($\male$) = components observed only in males, † = counts made from observations of female individuals only, †† = counts made from observations of male individuals only, - = component not observed. See text for explanation of "uninterrupted" data.

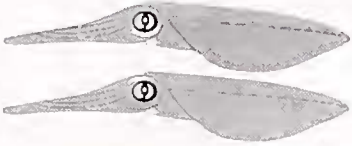Light Components:

1. Clear

2. White dorsal stripe
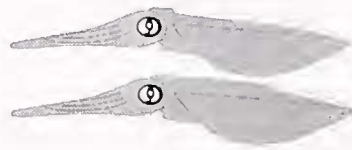
3. Golden epaulettes
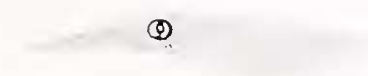
4. Iridescent sclera (♂ only)

5. Golden ocular epaulettes (♀ only)

Dark Components:

1. Plain

2. All dark

3. Dark mantle

4. Mantle margin stripe
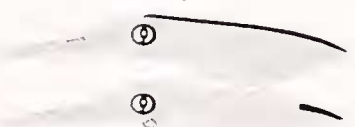
5. Fin stripe

6. Dark arm stripes (♂ only)

7. Stitchwork fins

8. Dark dorsal stripe

9. Mottled dorsal mantle

10. Dark posterior ventral mantle

11. Shaded eye

12. Bands

Figure 1.   Diagrammatic representation of chromatic components of body patterning in the squid *Sepioteuthis australis.*

1. Drooping arms

2. Rigid arms

3. Upward pointing
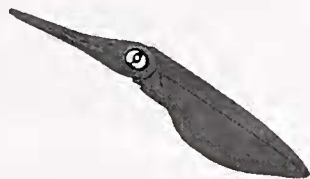
4. Downward pointing

5. Upward curl

6. Downward curl

7. Tentacle curl upward

8. Tentacle curl downward

9. Downward splayed arms (♂ only)

10. Lateral splayed arms (♂ only)

11. Raised arms

12. Curled tentacle club

13. Peristaltic arm flare *

14. Arms in mantle (♂ only)

15. Forward jetting arms

Figure 2. Diagrammatic representation of postural components of body patterning in the squid *Sepioteuthis australis*. Note: "Egg passing" has not been illustrated because it is distinguished by the peristaltic movement of the funnel held flat against the underside of the head. * = component is a transient posture consisting of the radial peristaltic flaring of the arms. Only the final stages of this component are represented by the illustration.

seconds immediately prior to "Male-upturned mating" (see below and Fig. 3). **Mantle margin stripe** (referred to as "Fin stripe" by Moynihan and Rodaniche; 1982, but here we follow the nomenclature of Hanlon *et al.*, 1999) was a darkened stripe running along the fin insertion the entire length of the mantle. **Fin stripe** (Hanlon *et al.*, 1994, 1999) occurred as a darkening of the edge of the fin. **Dark arm stripes** (referred to as "Dark third arms" by Porteiro *et al.*, 1990, and "Arm stripe (first or third)" by Hanlon *et al.*, 1994, but here we follow the nomenclature of Hanlon *et al.*,

Agonistic contests				Male-upturned mating			
Cl	4	Iridescent sclera (♂)		Cl	2	White dorsal stripe (♀)	
Cd	2	All dark (♂)		P	10	Rigid arms (♀)	
Cd	9	Mottled dorsal mantle (♂)		Cd	4	Mantle margin stripe (♂)	
P	11	Raised arms (♂)		Cd	5	Fin stripe (♂)	
				Cd	6	Dark arm stripes (♂)	
				Cd	11	Shaded eye (♂)	
P	10	Lateral splayed arms (♂)		P	2	Lateral splayed arms (♂)	
L	8	Parrying (♂)					
L	9	Fin beating (♂)					
L	10	Charging (♂)		L	12	Male-upturned mating	
Egg preparation				Head-to-head mating			
Cd	1	Plain (♀)		Cd	1	Plain	
P	16	Egg passing (♀)		L	13	Head-to-head mating	
L	3	Hovering (♀)					
Egg deposition				Male-parallel mating			
Cd	9	Mottled dorsal mantle (♂)		Cd	1	Plain	
P	4	Downward pointing (♀)		L	13	Head-to-head mating	
				Extra-pair Copulations			
P	7	Tentacle curl upward (♀)		Cl	2	White dorsal stripe (♂)	
				Cd	1	Plain (♂)	
P	13	Peristaltic arm flare (♀)		Cd	2	All dark (♂)	
L	7	Mate guarding (♂)					
L	11	Oviposition (♀)		L	15	Male "sneak" mating	

Figure 3. Components consistently identified in agonistic encounters, egg preparation, egg deposition, paired mating, and extra-pair copulations in *Sepioteuthis australis*. Numbers correspond to component numbers in Table 1; letters correspond to component types from Table 1; Cl = Light chromatic, Cd = Dark chromatic, P = Postural, L = Locomotor, (♀) = component shown by females; (♂) = component shown by males.
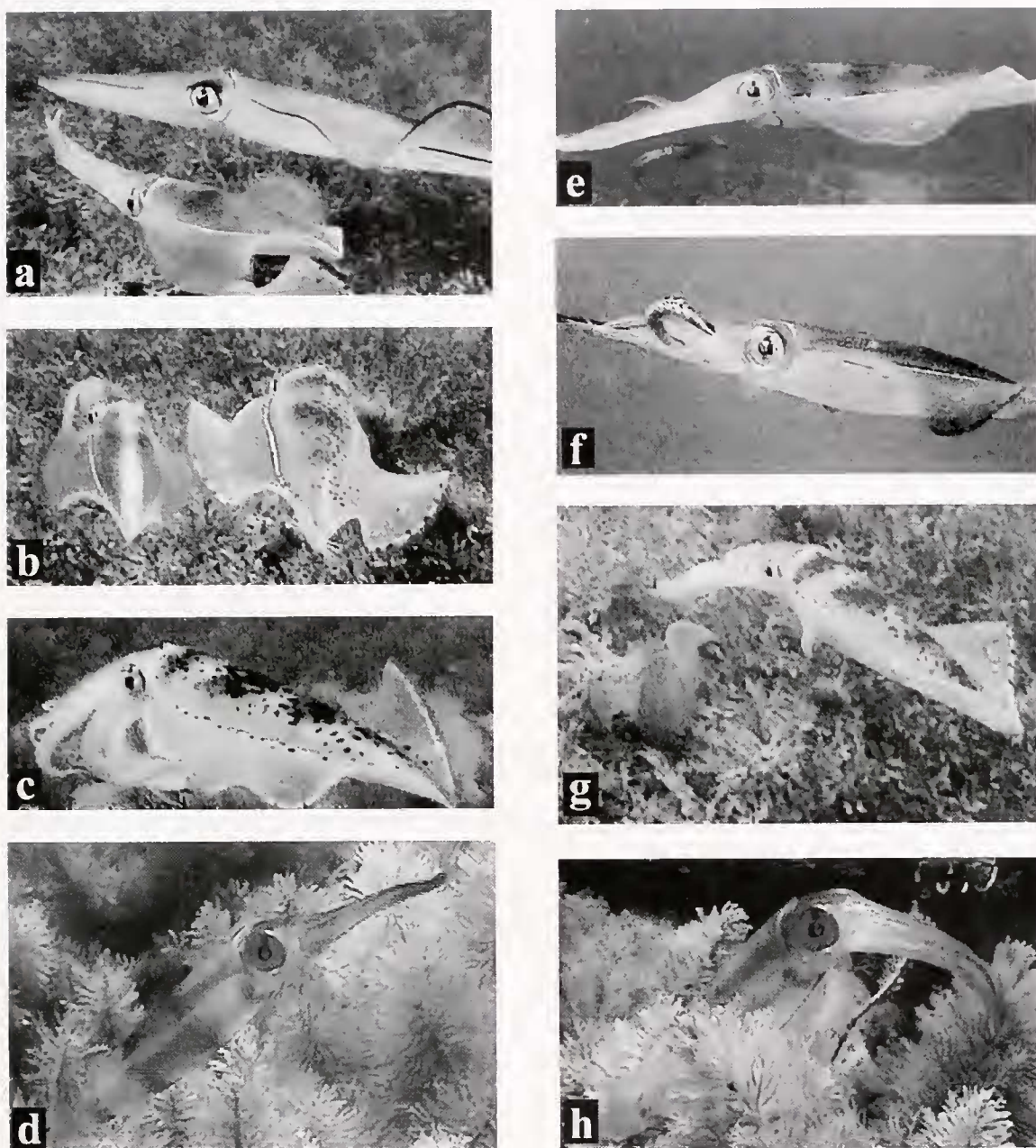
Figure 4. Selected typical body pattern components of *Sepioteuthis australis* taken from digital underwater video images. (a) Male (top) showing "Shaded eye," "Mantle margin stripe," "Fin stripe," "Dark arm stripes," and "Golden epaulettes." Female (Below) showing "Golden epaulettes". Male and female are "Parallel positioning". (b) Female (left) showing "White dorsal stripe" and "Golden epaulettes." Male (right) is showing "Mottled dorsal mantle," "Stitchwork fins," and "Golden epaulettes." Male and female are "Parallel positioning." (c) "Downward arm splay" of a male showing "Mottled dorsal mantle" and "Golden epaulettes." (d) Female showing "Bands" and "Golden epaulettes" while "Upward pointing," (e) Male showing "Raised arms" postural component with "Golden epaulettes," "Mottled dorsal mantle," and "Stitchwork fins" chromatic components. (f) "Curled tentacle club" with "Golden epaulettes." (g) Paired male (right) "Mate guarding" showing "Mottled dorsal mantle," "Golden epaulettes," and "Drooping arms." Only the posterior mantle of the female can be seen as she is "Downward pointing" in the process of "Oviposition" with her head amongst the seagrass substrate. (h) Female showing "Bands," "Downward curl," and "Upward pointing."

1999) involved the darkening of the most lateral arms and was shown exclusively by males (Table 1). **Shaded eye** was expressed as a transverse pigmented "bar" spanning the two eyes (as described in other squid species by Hanlon, 1988; Hanlon *et al.*, 1994, 1999) or as a shading immediately over the eye only. This component was common to both sexes (Table 1).

Stitchwork fins (Hanlon, 1982) comprised alternating black and white dashes that traversed the fins 2–3 cm from the edge. This component was one of the most common chromatic components shown by paired individuals (Table 1). **Dark dorsal stripe** was a darkened stripe along the center of the dorsal mantle. This component varied in length, either extending along the entire dorsal surface of the mantle or being shown only in the posterior region. We have few observations of this component (Table 1) and the behavior associated with it remains unclear. **Mottled dorsal mantle** was an irregular pattern of darkened spots on the dorsal mantle surface grouped together to form a mottle, occasionally extending to include the fins. Paired males showed this component in nonphysical agonistic encounters such as "Parrying" (see below). This component may be cryptic, as the irregularity of the pattern may disrupt the body shape when viewed from above (by predators). **Dark posterior ventral mantle** was an irregular darkening of the posterior ventral mantle (underneath the fins) up to a third of the length of the mantle in both sexes. This was more frequently seen in females (Table 1), but we remain uncertain of its behavioral significance.

Bands is also referred to as "Bars" by Moynihan and Rodaniche (1982) and Moynihan (1985) and as "Ring" by Hanlon (1982), but we follow the nomenclature of Hanlon *et al.* (1994, 1999) and Cornwell *et al.* (1997). This component was observed on all occasions as four transverse bands around the dorsal and ventral mantle. A single longitudinal stripe on the ventral mantle, similar to "Ventral mantle stripe" in *S. sepioidea* (Moynihan and Rodaniche, 1982), was also seen in conjunction with this pattern: because it was never observed independently, it is considered to be an integral part of the "Bands" component in *S. australis*. As in other loliginid squid, this component possibly aids in crypsis and was common in females of lone spawning pairs.

3. Postural components

Drooping arms occurred when the tentacles and arms of the individual were not in a "defined" posture and appeared limp. This component was reported by Hanlon *et al.* (1999) to occur in *Loligo pealei* individuals that were swimming, but we observed this behavior primarily in "Hovering" (see below) individuals of *S. australis* as well as in swimming ones. **Rigid arms** occurred when all arms and tentacles were held together immediately in front of the animal and

was the most common arm position of paired animals (Table 1). For consistency in the analysis, the transition from "Rigid arms" to "Drooping arms" was defined as the moment when the average angle of the arms and tentacles exceeded 45° downward from horizontal. **Upward pointing** and **Downward pointing** were scored when the orientation of the whole body exceeded 45° from horizontal in the respective direction. Both of these components were far more prevalent in females (Table 1). "Upward pointing" was more often seen in individuals close to the substrate while "Hovering," but "Downward pointing" was frequently observed in females that were "Forward swimming" (see below) prior to deposition of an egg capsule (Fig. 3). **Upward curl** and **Downward curl** were identical in posture to the descriptions given by Moynihan and Rodaniche (1982) for *S. sepioidea*. **Tentacle curl upward** was the simultaneous rolling back of the tip of the tentacles dorsally along the arms to form a tight circle with the suckers on the club facing out. This component always occurred in the seconds prior to "Oviposition" by the female (Fig. 3) and was a reliable predictor of egg deposition behavior. **Tentacle curl downward** was the rolling back of the tentacle tips downward, along the ventral surface of the arms with the suckers facing inward. This component was rare (Table 1), and the association with specific behaviors remains unclear.

Downward splayed arms (Fig. 4C) was observed only in males (Table 1). The arms and tentacles curled around posteroventrally from the "Rigid arms" posture so that each tentacle was offset from the next. The significance of this component remains unknown. **Lateral splayed arms** (as "Splayed arms" in Hanlon *et al.*, 1999) was recorded in the latter stages of a fight between males, usually coinciding with "Fin beating" (see below and Fig. 3). A series of these components in rapid succession ($<$ 1 s each) was also shown by several paired males poised above the female immediately prior to rotating to the upside-down position for "Male-upturned mating" (see below and Fig. 3). It is as yet unclear whether the duration of this component is significant in these different behaviors. **Raised arms** differed from the observations of this component in *L. pealeii* (Hanlon *et al.*, 1999) in that only the tips of the fourth pair of arms were raised, rather than the entire first pair of arms. This component was shown primarily by paired males (Table 1). As in *L. vulgaris reynaudii* (Hanlon *et al.*, 1994), this is thought to be an intraspecific agonistic signal because we consistently saw it in males that were "Parrying" (see below and Fig. 3).

Curled tentacle club was observed only in a single female; however, Jantzen and Havenhand (2003) previously identified this component in males of *S. australis* (as "Club display"). **Peristaltic arm flare** was a rapid component lasting for $\leq$ 1 s (Table 1) and involved the peristaltic flaring of the tentacles and arms from the base to the tips as the animal simultaneously pulsed a jet of water across the

arms (referred to as "Puffing" by Corner and Moore, 1980, and as "Cleaning maneuver" by Packard and Sanders, 1971). It appeared to be associated with the removal of excess matter from amongst the arms, and was most prevalent in females after "Oviposition" (Fig. 3). **Arms in mantle** occurred when all of the arms were positioned inside the ventral mantle while the tentacles adopted the "Drooping arms" posture. **Forward jetting arms** occurred when the arms and tentacles were directed posterioventrally coinciding with the rapid forward motion of the animal as it "Jetted" (see below) forward. **Egg passing** identifies a behavior in which females transferred eggs from the oviduct through the funnel into the arms. "Egg passing" was synonymous with the funnel being positioned flat against the underside of the head, with the funnel aperture opening into the bases of the arms. During this behavior, the ventral region of the arm bases enlarged as the eggs and egg capsule material were passed into the arms.

4. Locomotor components

Forward swimming, Backward swimming, Hovering, Jetting (Moynihan and Rodaniche, 1982; Hanlon et al., 1994, 1999), and **Turning** are self-explanatory. For consistency of analysis, **Parallel positioning** was defined here as paired squid aligned laterally and facing in the same direction, where any part of the bodies were closer than the paired male's body length. The high frequency of this component (Table 1) is indicative of the relative closeness of reproductively active pairs. **Mate guarding** is common in loliginid squids (Hanlon and Messenger, 1996) and was defined here as being a consort male within one body length of the female that was in the process of "Oviposition" (Fig. 3). Paired males frequently showed "Mottled dorsal mantle" while "Mate guarding."

The following three components are varying levels of agonistic encounters between males (Fig. 3). **Parrying** was the active positioning of the paired male between the female and an intruder male, within one body length of the intruder. No physical contact occurred between the intruder and paired male at this time. **Fin beating** (Hanlon et al., 1994, 1999; Jantzen and Havenhand, 2003) was the escalation of an agonistic contest into physical contact. The two males collided, beating their mantle and fins together. "Fin beating" consistently occurred with "Dark mantle" and "Iridescent sclera." **Charging** was defined as a rapid movement of a paired male toward a rival male, striking the intruder with the tentacles and radially flaring the arms. This is an intense agonistic encounter by a paired male and appeared similar to that described for *L. pealeii* (King et al., 1999) and *Loligo forbesi* (Porteiro et al., 1990).

Oviposition (Hanlon et al., 1999; Jantzen and Havenhand, 2003) denotes the process of egg deposition by a female (Fig. 3). **Male-upturned mating** (Jantzen and Ha-venhand, 2003) occurred when the male rotated laterally to an upside-down position above the female to mate. **Head-to-head mating** (Hanlon et al., 1999) occurred when the mating pair approached head-on and intertwined arms to mate. **Male-parallel mating** (Hanlon et al., 1994, 1999) occurred when the paired male approached the female from below and attempted to mate facing the same direction. "Plain" was the only chromatic component shown consistently throughout these prior two mating types (Fig. 3). **Male "sneak" mating** (Hanlon, 1994; Jantzen and Havenhand, 2003) was defined as any mating attempt by an unpaired male with a paired female. Sneaker males also commonly showed the "Plain" chromatic components, or (infrequently) "Dark mantle" and "White dorsal stripe" (Fig. 3).

Total component duration

The most prevalent chromatic component for both sexes was "Golden epaulettes" ("Chromatic Light 3" in Fig. 5), shown for more than 90% of the time. "Stitchwork fins" was also common in males (85% of the time; "Chromatic Dark 7" in Fig. 5), but was less prevalent in females. Other components prevalent in males were "Mottled dorsal mantle" (30%; "Chromatic Dark 9" in Fig. 5), and "Shaded eye" (20%; "Chromatic Dark 11" in Fig. 5). In females, "Shaded eye" (42%) and "Stitchwork fins" (22%) were also prevalent ("Chromatic Dark 11 and Chromatic Dark 7" in Fig. 5).

"Rigid arms" was the only postural component commonly shown by both sexes and was observed about 90% of the time ("Postural 2" in Fig. 5). "Raised arms" was also common in males (42%; "Postural 11" in Fig. 5).

The prevalences of the locomotor components "Forward swimming," "Backward swimming," and "Hovering" were much the same for both sexes ("Locomotor 1, 2, and 3" in Fig. 5). "Parallel positioning" occured ~ 50% of the time (both sexes; "Locomotor 6" in Fig. 5), and males spent 34% of the time "Parrying rival" males ("Locomotor 8" in Fig. 5).

Pairwise t tests of the differences in total component durations between males and females showed that only the durations of "Stitchwork fins" were significantly different (sequential Bonferroni test, table-wide $\alpha = 0.05$). Males showed this pattern for considerably longer periods (Fig. 5, Table 1).

Average component duration

Components that were shown by both males and females had a similar average duration. Only "Stitchwork fins," "Shaded eye," and "Raised arms" showed a large difference in average duration between the sexes ("Chromatic Dark 7," "Chromatic Dark 11," and "Postural 11" respectively; Fig. 6). However, variance was generally high, and pairwise t tests of the differences in average component durations

can be considered acute (lasting for seconds or minutes; *sensu* Box 3.1, Hanlon and Messenger, 1996). Several of these same components may also be considered chronic (lasting minutes to hours; *sensu* Hanlon and Messenger, 1996) when the maximum duration of each component is also considered (Table 1).
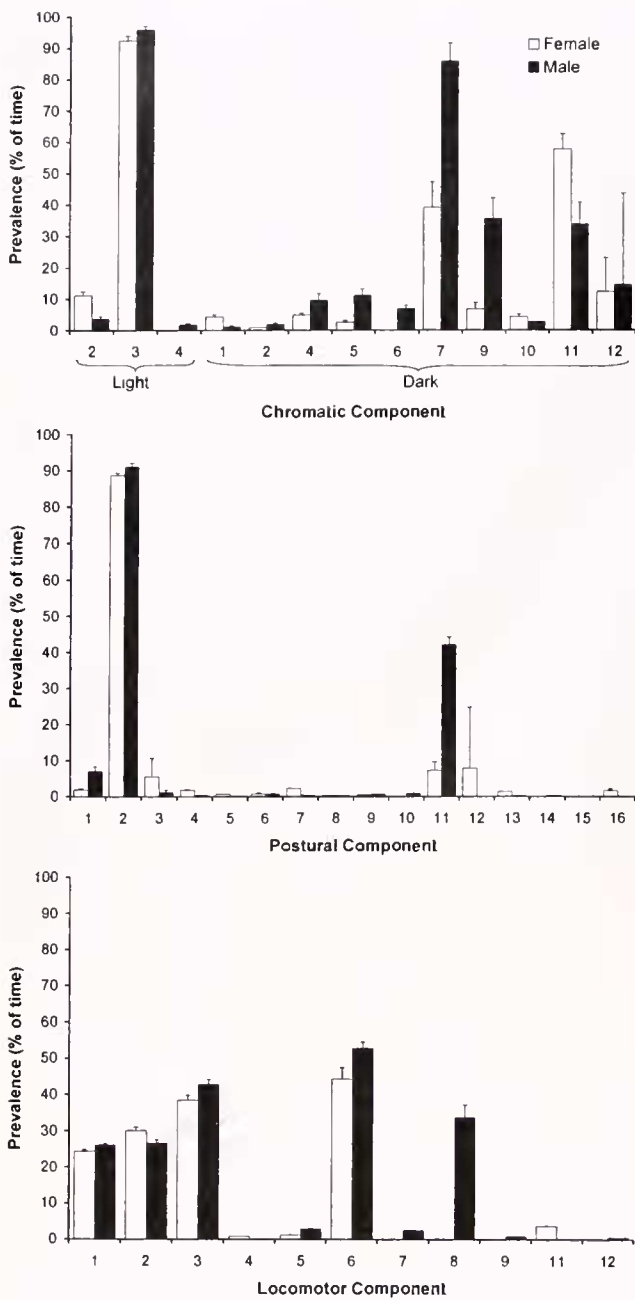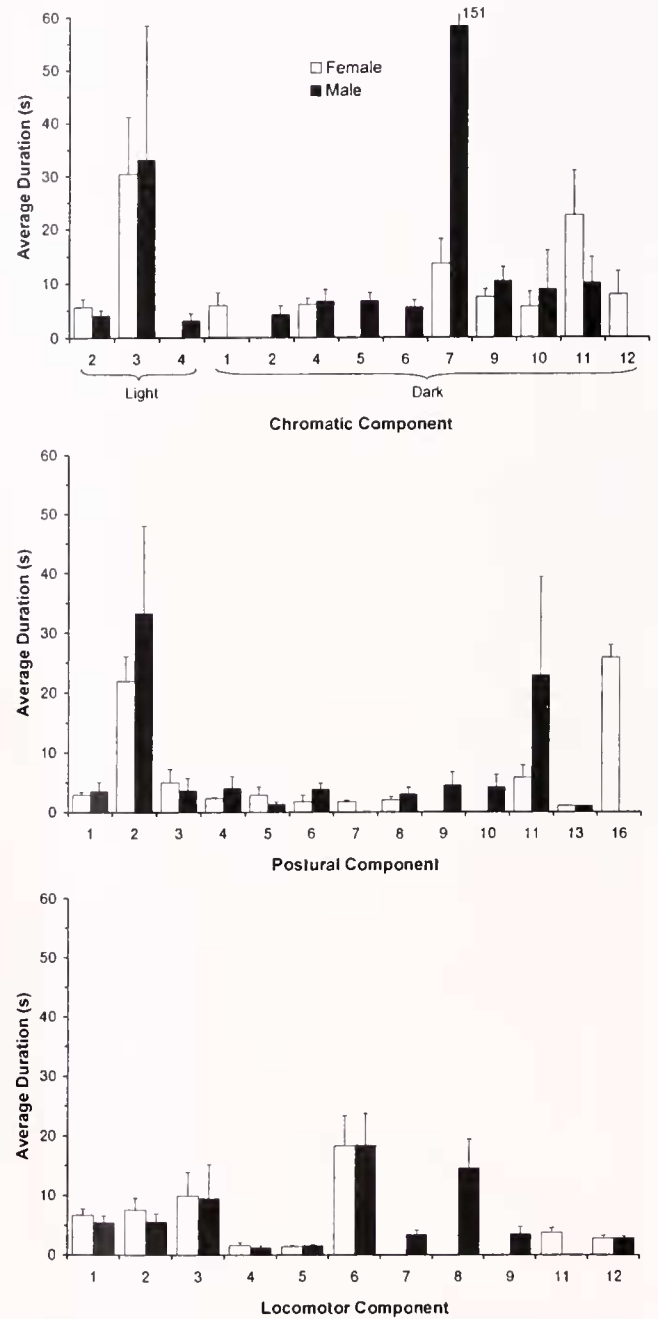

Figure 5. Prevalence (percent of total time observing each animal) of each chromatic, postural, and locomotor component identified in males and females of *Sepioteuthis australis*. Refer to Table 1 for component identification numbers. Error bars represent 95% confidence intervals ($3 \leq n \leq 11$).

between males and females showed that only "Forward swimming" differed significantly (sequential Bonferroni test, table-wide $\alpha = 0.05$).

Most (80%) of the components had an average duration less than 10 s (Fig. 7). 86% had durations less than 20 s, 95% were less than 30 s, and all were less than 60 s. Consequently, all of the components identified in this study

Figure 6. Average duration of each chromatic, postural, and locomotor component identified in females and males of *Sepioteuthis australis* (uninterrupted data only; see text for definitions). Refer to Table 1 for component identification numbers. Error bars represent 95% confidence intervals ($3 \leq n \leq 11$).
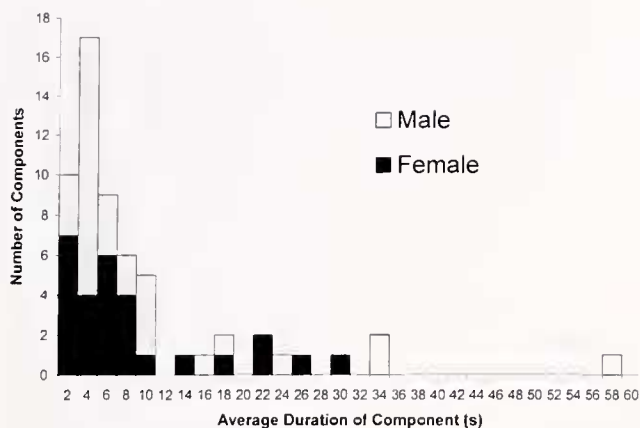
Figure 7. Stacked-column time: frequency distribution of average component duration in males and females of *Sepioteuthis australis*.

Discussion

All of the components we identified in *Sepioteuthis australis* had a mean duration less than 60 s (Figs. 5 and 6) and should therefore be classified as "acute" (*i.e.*, lasting for seconds or minutes, *sensu* Box 3.1, Hanlon and Messenger, 1996). However, because 80% of the components had a duration ≤ 10 s (Fig. 7), the classification may need to be refined to take account of varying levels of "acute" response. We propose a three-tier system consisting of short acute (≤ 10 s), medium acute (11–60 s), and chronic (> 60 s) component durations. Using this system, and treating the components shown by each sex separately, we classify 32% (25/77) of the components in *S. australis* as short acute, 43% (33/77) as both short acute and medium acute, and 25% (19/77) as short acute, medium acute, and chronic (Table 1). This system also permits identification of patterning differences that may be biologically meaningful. For example, components such as "Mottled dorsal mantle," "Drooping arms," and "Raised arms" all had acute durations (short and medium) in females of the species (Table 1), but these same components had chronic as well as acute (short and medium) durations in males. A thorough interpretation of these differences is beyond the scope of the present work; however, we believe that this additional distinction within "acute" will prove useful for interpreting the utilization of cephalopod component signals.

The ethogram of reproductive body components presented in this study has both similarities to and differences from those described for other species (Hanlon, 1988; Yang *et al.*, 1986; Porteiro *et al.*, 1990; Hanlon *et al.*, 1994, 1999). For example, similarities are seen in the "Clear" chromatic component, which was previously identified as an acute component by Hanlon (1988), Yang *et al.* (1986), Porteiro *et al.* (1990), and Hanlon *et al.* (1994, 1999) and also found here to be a short acute component in *S. australis*. Likewise, "Mate guarding" has been identified as an acute component

in *Loligo pealeii* (Hanlon *et al.*, 1999) and was also defined as an acute (short and medium) component here for *S. australis*. In contrast, "Dark dorsal stripe" (Hanlon *et al.*, 1994) has previously been identified only as a chronic component, but was identified in our study as a short acute component (Table 1, and see above).

The high number of short acute component durations we identified (Table 1, Fig. 6) indicates intense communication between reproductively active individuals and is probably important in competition for mates and in predator detection. Guilford and Dawkins (1991) have argued that short, intense animal signals (lasting only a few seconds) are more information-rich than longer, weaker signals. The corollary of the observed intensity of short acute component durations is that reproductively active individuals of *S. australis* showed few long (medium acute, or chronic) duration components (Fig. 6). It is possible that signals are communicated by relatively brief absences of these longer duration components (rather than by their chronic presence); however, their significance has yet to be determined.

"Golden epaulettes," "Stitchwork fins" (male only), and "Rigid arms" were all shown for over 80% of the total observation time (see Fig. 5), and these three same components also had the longest average durations (see Fig. 6). Because long component durations were more strongly affected than short durations by our procedure of counting only uninterrupted recordings, more than 80% of the data for "Golden epaulettes" and "Stitchwork fins" was omitted due to interruptions. Consequently, average durations in Figure 6 are probably a marked underestimate of the true durations for these components.

If the catalog of behaviors observed for a species is representative of the entire behavioral repertoire, then a plot of the cumulative rank-order percentage-time frequencies of the behaviors should show a marked asymptote (Lehner, 1979). Relevant plots for our data show an asymptote for both females and males after 30 components (Fig. 8). We identified 38 components for females and 44 for males (Table 1). These numbers exceed the point at which an asymptote is reached in each data set and therefore suggest that the data reported here are indeed a representative catalog of the component repertoire for the reproductive behavior of this species (Lehner, 1979).

The number of chromatic components we identified (*n* = 17) is less than that described for *S. lessoniana* (23; Moynihan and Rodaniche, 1982; Moynihan, 1985; Hanlon and Messenger, 1996) and *S. sepioidea* (23; Moynihan and Rodaniche, 1982; Hanlon and Messenger, 1996). However, our data for *S. australis* (17 chromatic components, Table 1) relate only to reproductive behavior. Of the 23 chromatic components reported by Moynihan and Rodaniche (1982) for *S. sepioidea*, 17 were observed in reproductively active individuals (*i.e.*, 75% of the total repertoire). In total, 23 chromatic components were also identified in *S. lessoniana*
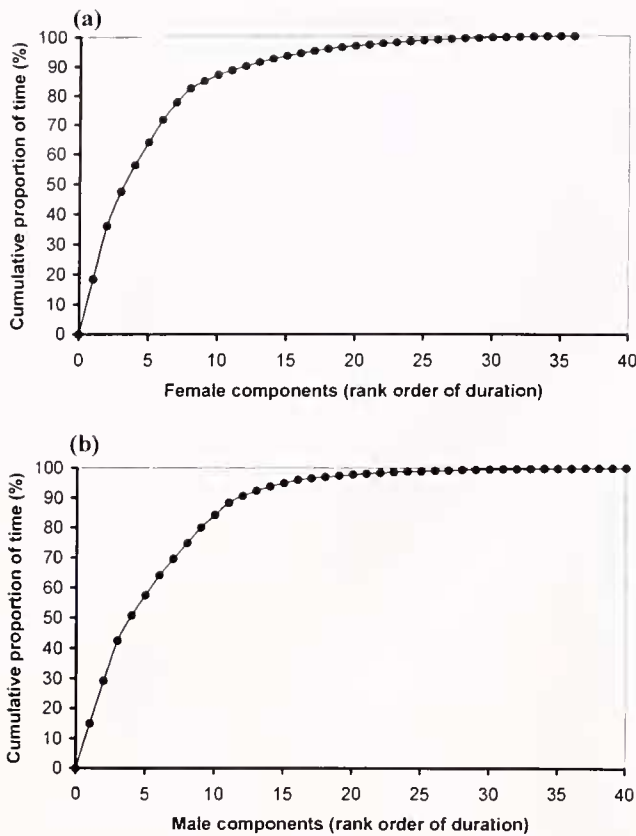
Figure 8. Plot of cumulative rank-order percentage-time frequencies plot of body pattern components identified in (a) females and (b) males of *Sepioteuthis australis*. Numbers on *x* axis refer to the ranked order of component numbers, not the assigned component numbers in Table 1.

(Hanlon and Messenger, 1996), although the number of these components specific to reproductive behavior is not known. We were unable to identify body pattern components associated with nonreproductive behavior, and therefore we do not know the full component complement for *S. australis*. Nonetheless, the full repertoire of chromatic components in cephalopods is thought to be correlated with habitat complexity (table 3.9 in Hanlon and Messenger, 1996). Given that *S. australis* lives in a structurally less complex habitat than *S. sepioidea* (seagrass *versus* coral reefs), it seems likely that the ethogram of reproductive components identified here is a large proportion of the entire ethogram for this species.

As in this current study, the body patterning behavior of *L. pealeii* (Hanlon *et al.*, 1999), and *L. vulgaris reynaudii* (Hanlon *et al.*, 1994) was described primarily from individuals on spawning grounds. It is therefore useful to compare the ethograms of these two *Loligo* species with that of *S. australis*. For *L. pealeii*, 30 chromatic, 5 postural, and 12 locomotor components (plus a further 4 polarized components) were identified (Hanlon *et al.*, 1994); for *L. vulgaris reynaudii*, the numbers were 23 chromatic, 4 postural, and

9 locomotor components (Hanlon *et al.*, 1994). It seems that these two *Loligo* species have a larger repertoire of chromatic components than *S. australis* has, but the repertoire of postural and locomotor components appears considerably larger for *S. australis*. Differences in chromatic component numbers can probably be attributed to differences in habitat structural complexity (table 3.9 in Hanlon and Messenger, 1996), but the significance of differences in postural and locomotor component numbers between species is unclear.

When comparing the ethograms of *L. pealeii* (Hanlon *et al.*, 1999), *L. vulgaris reynaudii* (Hanlon *et al.*, 1994), and *S. australis*, many of the component patterns appear similar, but the comparative frequency that each component is shown varies markedly. The prevalence of some components is quite different between all three species. For example, "All dark" was the most prevalent dark chromatic component shown by *L. pealeii* (Hanlon *et al.*, 1999), it was shown moderately by *L. vulgaris reynaudii* (Hanlon *et al.*, 1994), and it was one of the least common dark chromatic components shown by *S. australis* (Table 1). Alternatively, the display frequency of some components shows signs of differentiation between the two genera. For example, "Clear" was frequently shown by both *L. pealeii* (Hanlon *et al.*, 1999) and *L. vulgaris reynaudii* (Hanlon *et al.*, 1994), but was the least shown light chromatic component for *S. australis*. Body pattern components of behavior are thought to be useful in taxonomic distinction between squid species (Hanlon, 1988; Roper and Hochberg, 1988), and discussions such as the above demonstrate some of the comparisons that can be made.

As well as comparisons of ethograms between species, comparisons between members of a species that are and are not reproductively active could provide an important insight into the visual vocabulary associated with spawning. Anecdotal observations of non-reproductively active (feeding) squids showed that the most common postural component (> 50%) was "Downward pointing" (perhaps as an aid to prey acquisition). We observed the "Downward pointing" posture in reproductively active individuals only in females and only for 2% of the total time (Fig. 5); it generally occurred when the female was seeking out the egg cluster on the substratum prior to egg deposition. Consequently, while our analysis suggests that the ethogram of reproductive components presented here adequately describes the reproductive body patterns of *S. australis*, it seems equally clear that this ethogram does not describe the suite of body patterns exhibited by non-reproductively active individuals.

In a previous study, we reported that "Curled tentacle club" (as "Club display"; Jantzen and Havenhand, 2003) was shown by a male to the female as a signal of intention to mate. It is now clear that this was incorrect. Firstly, all 84 incidences of "Curled tentacle club" in this study were in females (Table 1); secondly, the frequency of this component was not related to copulation frequency.

Each of the four mating types reported here for *S. australis* ("Male-upturned mating," "Head-to-head mating," "Male-parallel mating," and "Male 'sneak' mating") had a maximum duration of 4 s (Table 1). It cannot be ruled out that "Male-upturned mating" and "Head-to-head mating" are derivatives of the same mating type, as it is likely that the site of spermatophore deposition is in the arms for both these mating types. However, because the deposition site for "Head-to-head mating" in *S. australis* could not be identified here, we believe these two mating types should be considered as separate behaviors. Interestingly, "Male-upturned mating" was the most common mating type observed here (20 out of 29 matings; Table 1). This mating type has been observed in only one other species of squid (*S. lessoniana*) and only in the laboratory (Boal and Gonzalez, 1998). Those authors report a mating duration similar to that reported here (3 s; Table 1, Fig. 6). Durations of other mating types seen here were also comparable to those observed in other squids (see Segawa *et al.*, 1993; table 6.2 in Hanlon and Messenger, 1996). This suggests that the durations of these behaviors in different species may have evolved in response to similar selective pressures.

Identifying the selective benefits of a given patterning component or behavior is difficult. For example, immediately prior to mating, paired males of *S. australis* always showed "Mantle margin stripe," "Fin stripe," "Dark arm stripes," and "Shaded eye" chromatic components. This proved to be a reliable predictor of a "Male-upturned mating" attempt (Fig. 3). However in *Loligo vulgaris reynaudii*, "Fin stripe," Mantle margin stripe," and "Arm stripes" are all intraspecific signals in agonistic contests between males (Hanlon *et al.*, 1994). Boal (1997) suggested that the mating displays of male cuttlefish function as agonistic signals to other males rather than courting signals to females. Whether these components portray different messages in these two species, or are used agonistically towards other males during mating in *S. australis* is unclear.

"Lateral splayed arms" was shown by males of *S. australis* in association with "Male-upturned mating" as well as in agonistic encounters with rival males. This signal has been identified as exclusively agonistic in *L. vulgaris reynaudii* (Hanlon *et al.*, 1994), *L. plei* (DiMarco and Hanlon, 1997), and *L. pealeii* (Hanlon *et al.*, 1999), although in *S. sepioidea* it is reportedly both agonistic (Moynihan, 1985; Hanlon and Messenger, 1996) and associated with mating (Moynihan and Rodaniche, 1982). Again, it is possible that this component portrays different messages in different species; however, it is also possible that the duration of this component differs subtly between mating and agonistic behaviors. We could not distinguish any consistent differences from our analyses, so this possibility remains to be tested.

In contrast to reports in the literature, we found that mating types were not used consistently within males. In-

deed, some males copulated with the same female in all three paired mating positions ("Male-upturned mating," "Head-to-head mating," and "Male-parallel mating"). Previously, no more than three mating positions had been reported within a single squid species (table 6.2 in Hanlon and Messenger, 1996). Whether paired males of *S. australis* show (or have shown) "Sneaker mating" at other times is not known; however, this evidence suggests that *S. australis* may exhibit a greater diversity in mating positions (three, plus "Sneaker mating") than other squids.

We identified three types of agonistic encounters between rival males: "Parrying," "Fin beating," and "Charging" (Fig. 3). While "Parrying" represented a nonphysical intraspecific encounter, "Fin beating" and "Charging" involved physical contact between rival males. "Parrying" (34% of time, Fig. 5; 334 observations, Table 1) was far more prevalent than "Fin beating" (1% of time, Fig. 5; 32 observations, Table 1) and "Charging" (7 observations, Table 1). In addition, "Parrying" had a longer average duration (15 s, Fig. 6) than "Fin beating" (4 s, Fig. 6). This behavior is similar to the fighting tactics of *L. plei* in which physical agonistic contests between rival males are shorter than nonphysical contests (DiMarco and Hanlon, 1997).

In a wider context, chromatic components of behavior are useful in taxonomic distinction of squid species (Hanlon, 1988; Roper and Hochberg, 1988). Comparative allozyme analysis of *S. australis* has identified a discrete genetic divergence between the New Zealand and Australian populations (Triantafillos and Adams, 2001). It is possible that these populations have also evolved a different repertoire of reproductive components. The only report of the reproductive behavior of *S. australis* from New Zealand (Larcombe and Russell, 1971) describes body components generally consistent with "Clear," "Hovering," "Parallel positioning," "Rigid arms," "Oviposition," "Mate guarding," "Downward pointing," "Plain," "Peristaltic arm flare," "Charging," and "Parrying"; unfortunately, their descriptions lack sufficient detail to be directly compared with our observations. Further comparative research on the repertoire, frequency, and duration of reproductive components between these two populations would be valuable. Not only would this aid our understanding of the evolution of behavioral mechanisms or reproductive isolation in cephalopods, but it would also cast considerable light on the behavioral differences between populations of the species observed here.

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